ZOARIAL MICROSTRUCTURES OF TWO PERMIAN SPECIES OF THE BRYOZOAN GENUS *STENOPORA*

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ABSTRACT. The zooecial walls of *Stenopora ovata* Lonsdale and *S. crinita* Lonsdale consist of laminae which are built of variably shaped and variably disposed tabular units. It is suggested that the acanthopores of *S. crinita* and *S. ovata* are rods of calcite that together with the surrounding wall laminae were deposited by the stenoporid zooids. The mechanisms of growth of the laminae and their components are discussed.

TRADITIONALLY the laminae that comprise the skeletons of members of the bryozoan orders Cyclostomata, Trepostomata, Cryptostomata, and Cystoporata (i.e. Boardman's and Cheetham's (1969) tubular Bryozoa) have been interpreted as growth surfaces. Laminae were believed to have been added to the skeleton one layer at a time with the depositing epithelium paralleling the laminae. However, Boardman and Cheetham (1969) have now recognized exceptions to this growth model in Pliocene to Recent heteroporid Cyclostomata. Whereas the wall laminae of many tubular Bryozoa are convex distally (e.g. *Stenopora* herein), the laminae making up the walls of these heteroporid skeletons, together with the appearances of the skeletal components on zooecial surfaces, suggest that calcium carbonate was added simultaneously to the exposed edges of numerous laminae. Such laminae enlarge in an edgewise direction and are oblique to growth surfaces. For zoaria having distally convex wall laminae, Boardman and Towe (1966) had suggested that the laminae were in fact deposited layer by layer, each layer being essentially completed before the succeeding one was initiated. In this scheme, the depositing epithelium parallels the laminae that it is secreting. Nevertheless, as a result of their findings from Recent heteroporid specimens, Boardman and Cheetham (1969) speculated that 'quite possibly many Bryozoa having laminae that closely parallel depositing epidermis will prove to have shingled and edgewise crystal development'.

Results presented herein were obtained from a study of two species of the trepostomatous genus *Stenopora* in which the wall laminae are convex distally. The work was undertaken to detail the characteristics of laminar parts of the skeletons of these species and to determine the nature of acanthopores which occur in the zooecial walls. One specimen (F15872) of *Stenopora ovata* Lonsdale and one specimen (F60038) of *Stenopora crinita* Lonsdale were used; both specimens now being retained in the type collections of the Department of Geology, University of Queensland. The illustrations in Plates 112 and 113 are optical photomicrographs of thin sections and the photographs in Plates 114 to 117 are electron-micrographs of polished sections (Pl. 114–16) and broken skeletal surfaces (Pl. 117). The polished sections were cut perpendicular to (transverse section) and parallel to (vertical section) the direction of growth of the zooecia. The surfaces of the sections were polished with a sequence of abrasives finishing with a 1-μm. diamond abrasive. Before replication, the surfaces of the sections were etched for a few seconds with a mixture of 1% nitric acid in ethyl alcohol. The normal two-stage carbon replicating technique was employed; the intermediate medium being nitrocellulose. The broken surfaces used were obtained by splitting the zooecial walls and directly replicating, without any polishing or etching, the fractured surface. Shadowing of the replicas at angles of approximately 30° was with 1 to 1 mixtures of gold and palladium.

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ZOARIAL STRUCTURE

The zoaria of *Stenopora ovata* and *S. crinita* consist of zooecial tubes separated by laminar walls containing acanthopores.

The zoarium of the studied specimen of *Stenopora crinita* is massively branching with a broad immature zone surrounded by a mature zone about one half as wide. The branches are up to 8 cm. in diameter. Zooecial tubes are polygonal and their walls are usually thin (Pl. 113, fig. 7). No diaphragms are present in any of the zooecia and annular thickenings of the walls occur only in the mature zone where they are small and widely separated. Acanthopores are present only at wall junctions.

The zoarium of the studied specimen of *Stenopora ovata* is encrusting a brachiopod shell and is about 1 cm. thick. Zooecial tubes are polygonal to smoothly rounded and lack diaphragms. Annular thickenings of the walls are well developed throughout the zoarium (Pl. 113, figs. 3, 4). Acanthopores are present only at wall junctions (Pl. 112, figs. 1–3).

LAMINAR MICROSTRUCTURE

The zooarial walls of *Stenopora* are composed of laminae of the order of 1–5 μm. thick (Pl. 115, fig. 6; Pl. 117, figs. 1–4). In vertical sections perpendicular to the walls the laminae are convex distally (Pl. 113, figs. 3, 4, 6; Pl. 114, fig. 2; Pl. 115 figs. 1, 2: Pl. 116, figs. 1–3). Laminae successively overlie each other both in the walls and annular thickenings and they terminate at the surfaces of the walls (Pl. 113, figs. 3, 4, 6; Pl. 114, figs. 1, 2; Pl. 115, fig. 2). In transverse section the laminae are also arched and they are convex away from the closest inter-zooecial angle (Pl. 114, fig. 1; Pl. 115, fig. 3). Because the laminae are convex distally, transverse sections of the zooecia often show the walls with apparently non-laminated central regions bordered on each side by a zone having an obvious laminar structure (Pl. 114, fig. 1). This apparent layering of the wall is simply the result of sectioning a series of parallel sharply convex laminae. Towards the surfaces of the walls the laminae are perpendicular to transverse sections, whereas medially the tangential relationship between the wall laminae and the section yields the massive appearance of this part of the wall. Adjacent to acanthopores the laminae are deflected distally (Pl. 113, figs. 1, 2, 5) and they comprise a series of 'cone-in-cone' structures. Transverse sections usually reveal the laminae concentrically arranged around acanthopores (Pl. 112, figs. 1, 2; Pl. 114, fig. 5; Pl. 115, figs. 4, 5) although in the walls of the specimen of *Stenopora crinita* this concentric arrangement is not developed except

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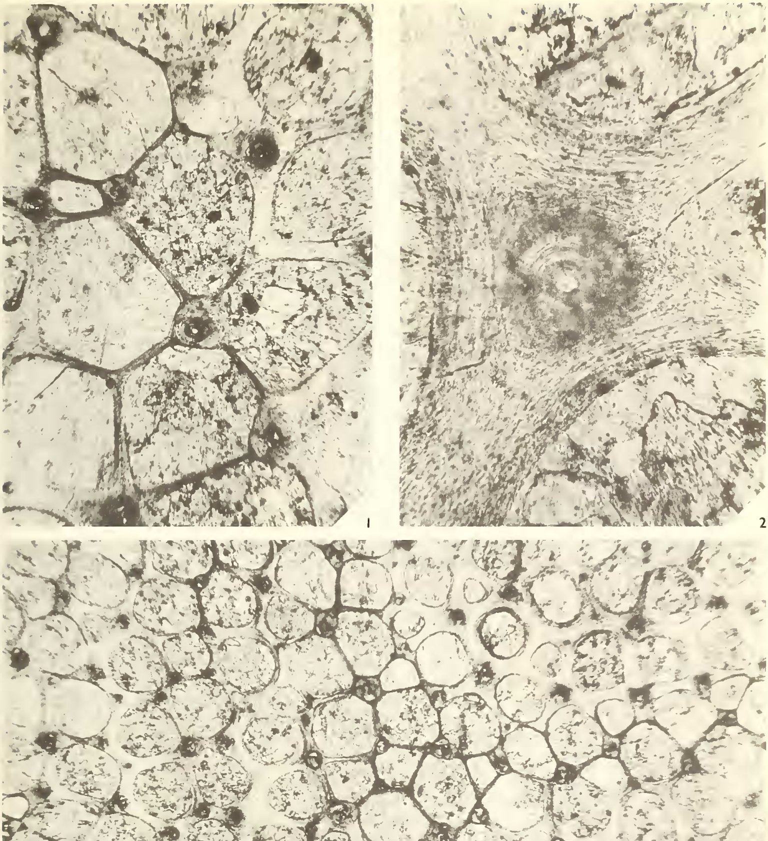
EXPLANATION OF PLATE 112

Figs. 1–3. *Stenopora ovata* Lonsdale. F15872, transverse sections of the zoarium illustrating zooecia and acanthopores. 1, ×60. 2, ×250. 3, ×25.

EXPLANATION OF PLATE 113

Figs. 1–5. *Stenopora ovata* Lonsdale. F15872. 1, vertical section parallel to wall illustrating an acanthopore and the adjacent inclined wall laminae, ×95. 2, enlargement approximately by 3 of part of the acanthopore in fig. 1. 3, 4, moniliform appearance of zooecial walls in vertical section, both ×85. 5, vertical section parallel to wall illustrating acanthopores and wall laminae, ×60.

Figs. 6 and 7. *Stenopora crinita* Lonsdale. F60038. 6, vertical section of thickened portion of a zooecial wall illustrating disposition of the wall laminae, ×60. 7, transverse section of zoarium illustrating the thin walled polygonal zooecia with inorganic lining, ×20.



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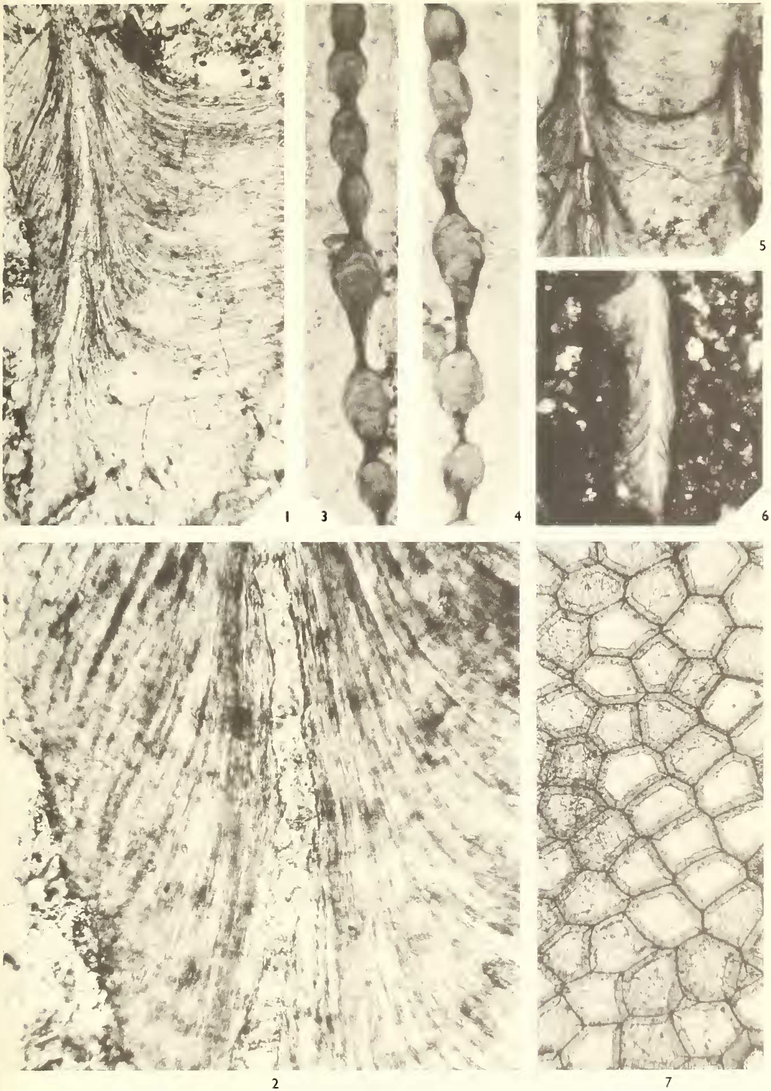

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in thicker parts of the walls (Pl. 114, figs. 3–5). Growth-lines and annular thickenings in the walls of the zooecia of *Stenopora ovata* and *S. crinita* are concave distally reaching their most distal points at the inter-zooecial wall junctions (Pl. 113, fig. 5).

Longitudinal sections of the walls immediately distal to the annular thickenings of *Stenopora crinita* show the wall with a massive central portion that is surrounded by one or more laminae, the number of laminae increasing distally (Pl. 116, figs. 1–3). This massive material was present above all of the examined annular thickenings of *S. crinita* and although its origin is conjectural, the consistent appearance of the material seems to suggest that it was a primary deposit laid down by the stenoporid zooids. Similar massively granular regions occur above some of the annular thickenings of *Stenopora ovata* (Pl. 115, figs. 1, 2). Above other annular thickenings of *S. ovata* there appear to be superimposed laminae like those in normal parts of the walls.

The components making up the laminae of *Stenopora crinita* were observed in replicas of broken surfaces of the walls. The laminae are built of tabular units which are two to five times wider than they are thick, and twice to many times longer than they are wide (Pl. 117, figs. 1–4). Boundaries between the tabular units of a lamina are marked by grooves in the surface of the lamina. The laminae consist of both irregularly and regularly shaped units. Surfaces of the laminae sometimes bear ridges, and these seem to be associated only with the more regular laminar units (Pl. 17, figs. 1, 2). The surfaces of the regular units are also often marked with fine chevron-shaped ridges and grooves (Pl. 117, figs. 1, 2). Armstrong (1969) described a somewhat similar situation in the shells of the strophomenid brachiopods *Streptorhynchus pelicanensis* and *Terrakea solida*. The shells of these species consist of thin sheets, each of which is composed of tabular blade-like units. The blades of a particular sheet are parallel to each other, but almost invariably they are not parallel either to the blades in contiguous sheets above and below or to the blades in adjacent coplanar sheets. Surfaces of the sheets are covered with crossing sets of parallel ridges and grooves (Armstrong 1969, pl. 57, fig. 3; pl. 58, figs. 1, 2), the grooves representing the boundaries between the blades of that sheet and the ridges being the parts of that sheet which have infilled the inter-blade grooves in the base of the sheet above.

ACANTHOPORES

Commonly occurring in the skeletons of bryozoans are structures referred to as acanthopores. Bassler (1953) defined an acanthopore as a ‘cylindrical tube adjoining zooecial walls and parallel to them in growth; formed of cone in cone layers with narrow central tubule which may be crossed with minute diaphragms; position often marked superficially by projecting spines’, and he stated that they ‘undoubtedly represent zooids with some definite function’ (Bassler 1953, p. G 91). Previously, in discussing the morphology of trepostomatous zoaria, Cumings and Galloway (1915) had referred to acanthopores as ‘hollow thick walled tubules’. They speculated that the small spines formed by the projection of acanthopores beyond the surface of the zoarium had a protective function (Cumings and Galloway 1915, pl. 15, figs. 51, 52). Subsequent to Bassler (1953) many references to, and definitions of, acanthopores have implied their tubiform nature Boardman 1960, pp. 28, 29; Ross 1961, pp. 21, 32, text-fig. 7; Ross 1966, p. 112; Boardman and Utgaard 1966, p. 1087; Cuffey 1967, p. 53). Recently, however, Tavener-Smith (1969) has suggested that acanthopores in the